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1 Olive baboons, *Papio anubis*, adjust their visual and auditory intentional gestures to the visual
2 attention of others

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19 Although nonhuman primates' gestural communication is often considered to be a likely
20 precursor of human language, the intentional properties in this communicative system have
21 not yet been entirely elucidated. In particular, little is known about the intentional nature of

22 monkeys' gestural signalling and related social understanding. We investigated whether olive
23 baboons can (1) adjust their requesting gestures to the visual attention of the experimenter
24 with special emphasis on the state of the eyes (open versus closed), and (2) flexibly tailor
25 visual and auditory-based gestures to elaborate their communication as a function of whether
26 or not the experimenter can see them. Using a food-requesting paradigm, we found monkeys
27 able to favour either visual or auditory-based requesting gestures to match the experimenter's
28 visual attention. Crucially, when the human was not visually attending, they silenced visual
29 gestures to some extent but performed more attention-getting gestures. This is, to our
30 knowledge, the first report of monkeys elaborating attention-getting signals to compensate for
31 communication breakdown. Gestural communication was also supported by gaze alternation
32 between the experimenter's face and the food, especially when the human was visually
33 attending. These findings offer evidence that olive baboons understand the state of the eyes in
34 others' visual attention and use requesting gestures intentionally. They emphasize that Old
35 World monkeys shift to acoustic communication when the recipient is not visually attending.
36 In contrast to that of human infants and great apes, this acoustic communication is purely
37 gestural, not vocal.

38

39 **Keywords**

40 audience attention, gestural communication, intentionality, language, nonhuman primate

41

42 Intentional communication is collaborative in essence since it requires mutual attention from
43 both parties in the interaction (Tomasello, Carpenter, Call, Behne, & Moll, 2005). When
44 producing gestural requests such as pointing gestures, the sender should be able to perceive
45 the visual attention of the recipient (Butterworth, 2004). In human infants, taking a partner's

46 attentional state into account when gesturing is seen only from around 15 months of age
47 (Bates, Camaioni, & Volterra, 1975; Franco & Butterworth, 1996; Leavens & Hopkins,
48 1999). The best evidence of an understanding of attention in children is the coordination with
49 others' attention to external targets, also called 'joint attention' (Butterworth, 2004; Scaife &
50 Bruner, 1975). This ability is considered critical for the development of both language and the
51 ability to attribute mental states to others (Camaioni, Perucchini, Bellagamba, & Colonnesi,
52 2004; Reddy, 2004).

53 Nonhuman primates do communicate with gestures too. A communicative gesture has
54 recently been defined as 'any non-vocal bodily action directed to a recipient that is
55 mechanically ineffective and represents a meaning, beyond itself, that is in part manifested by
56 others of the social group' (Scott & Pika, 2012, p. 158; but see Perlman, Tanner, & King,
57 2012 for an alternative view of mechanical effectiveness). Great apes and cercopithecines
58 produce these communicative signals, and so far research has mostly emphasized their use,
59 function and language-like properties (Pika & Liebal, 2012). Indeed, this gestural system of
60 communication is often considered to be the most likely precursor of human language
61 (Corballis, 2003; Pollick & de Waal, 2007; Vauclair, 2004) owing to shared similarities such
62 as the flexible and voluntary use of gestures (Liebal & Call, 2012; Meguerditchian, Cochet, &
63 Vauclair, 2011), or the brain specialization for gesturing (Corballis, 2003; Hopkins &
64 Vauclair, 2012). However, whether nonhuman primates gesture with the genuine intent to
65 modify their recipient's behaviour, attention or knowledge has not yet been entirely
66 elucidated (Gómez, 2007). Although there is solid evidence that great apes are sensitive to
67 their partner's attentional state when gesturing, little is known about the intentional nature of
68 monkeys' gestural signalling and related social understanding (Call & Tomasello, 2007; Scott
69 & Pika, 2012). Specifically, for both great apes and monkeys it is not clear whether the
70 relevant cues to attention of the recipient are the eyes or more general indicators such as head

71 and body orientation (Emery, 2000; Povinelli & Eddy, 1996; Povinelli, Eddy, Hobson, &
72 Tomasello, 1996; but see Kaminski, Call, & Tomasello, 2004).

73 Deictic gestures that refer to external targets are used by nonhuman primates to
74 perform requests (Gómez, 2005; Pika, 2008). To be considered as intentional, they must fulfil
75 several criteria used for prelinguistic children's pointing (Bates et al., 1975; Leavens, 2004):
76 (1) the gesture is goal-oriented and the signal persists or is completed with other signals until
77 the desired outcome is reached; (2) the gesture is adjusted in accordance to the attentional
78 state of the audience, whose attention can be regained by the use of additional attention-
79 getting behaviours; and (3) the gesture is supported by visual orienting behaviours alternating
80 between the recipient and the distal object of interest (gaze alternation). Evidence is
81 accumulating that great apes use visual gestures only if the recipient is visually attending (e.g.
82 bonobos, *Pan paniscus*: Pika, Liebal, Call, & Tomasello, 2005; orang-utans, *Pongo*
83 *pygmaeus*: Liebal, Pika, & Tomasello, 2006; gorillas, *Gorilla gorilla*: Genty, Breuer,
84 Hobaiter, & Byrne, 2009; chimpanzees, *Pan troglodytes*: Hobaiter & Byrne, 2011) and persist
85 with (e.g. Genty & Byrne, 2010; Liebal, Call, & Tomasello, 2004) or elaborate (Cartmill &
86 Byrne, 2007; Leavens, Russell, & Hopkins, 2005) their gestures until they achieve a certain
87 goal. However, attempts to determine which cues to attention are used by apes and monkeys
88 to adjust their communication have led to mixed results. While it is often not possible to
89 characterize the state of the eyes of individuals in naturalistic settings (e.g. Emery, 2000;
90 Genty et al., 2009), experimental studies have further demonstrated that nonhuman primates
91 generally use body orientation (e.g. great apes: Hostetter, Cantero, & Hopkins, 2001;
92 Kaminski et al., 2004; Povinelli et al., 1996; monkeys: Hattori, Kuroshima, & Fujita, 2010;
93 Meunier, Prieur, & Vaclair, 2012) or face orientation (e.g. great apes: Tempelmann,
94 Kaminski, & Liebal, 2011; monkeys: Maille, Engelhart, Bourjade, & Blois-Heulin, 2012) as
95 an indicator of a human's attention, although they may sometimes use face orientation only

96 when the human's body is oriented towards them (e.g. chimpanzees: Kaminski et al., 2004).
97 However, there is little evidence that nonhuman primates adjust their signals to the open and
98 directed state of the recipient's eyes (but see Hattori et al., 2010; Hostetter, Russell, Freeman,
99 & Hopkins, 2007). Instead, many studies have failed to demonstrate that subjects tailor their
100 gestural signals as a function of the state of the experimenter's eyes (Kaminski et al., 2004;
101 Povinelli et al., 1996; Theall & Povinelli, 1999). Although chimpanzees have been reported to
102 move into someone's visual field before starting to gesture rather than using auditory or
103 tactile signals to regain attention (Liebal, Call, Tomasello, & Pika, 2004), two studies showed
104 that chimpanzees favoured the modality of communication that best fitted the experimenter's
105 visual attention (Leavens, Hostetter, Wesley, & Hopkins, 2004), using auditory signals
106 specifically when the experimenter could not see them (Hostetter et al., 2007). While this may
107 constitute the best evidence so far that great apes can finely tune their gestures to the level of
108 attention of the recipient, there is no such evidence for monkeys, to which this stringent
109 paradigm remains to be applied.

110 We addressed this question in olive baboons using a food-requesting paradigm.
111 Baboons use two distal threat gestures in their natural communication, i.e. 'slapping ground'
112 and 'rubbing ground' (Estes, 1991; Kummer, 1968), usually performed towards an obviously
113 attending partner (Meguerditchian & Vauclair, 2006; Meguerditchian et al., 2011). They are
114 further known to rely on the use of gaze cues by conspecifics for soliciting help in conflicts
115 (Packer, 1977) and for deceptive communication (Whiten & Byrne, 1988). In experimental
116 settings baboons gestured more towards a human facing them than one oriented away
117 (Meunier et al., 2012), but no study has disambiguated which cues to attention they relied on.

118 We manipulated the experimenter's visual attention by varying the orientation of the
119 experimenter's whole body, including head (front/back), and the state of her eyes
120 (open/closed). We then addressed whether baboons (1) adjust their requesting gestures to the

121 visual attention of the experimenter with special emphasis on the state of her eyes, and (2)
122 flexibly tailor visual and auditory signals to elaborate their communication as a function of
123 whether or not the experimenter can see them. If baboons are able to use the state of the eyes
124 as a cue to visual attention, they should produce more requests when the experimenter's eyes
125 are open than when they are closed. If they not only use the state of the eyes as a cue to
126 attention, but also understand the role of open eyes as an attentional state that is specific to
127 their visual behaviour, baboons should tailor their gestural communication to the visual
128 attention of the experimenter, and therefore produce more auditory-based gestures than visual
129 gestures when the experimenter cannot see them compared to when she can. However, if
130 baboons rely on more general cues to attention such as body orientation, they should produce
131 more requests when the experimenter is facing them than when the experimenter is oriented
132 away.

133

134

135 <H1>Methods

136 <H2>Subjects

137

138 The experiments took place in the Primate Station of the Centre National de la Recherche
139 Scientifique (UPS 846, Rousset, France; Agreement number for conducting experiments on
140 vertebrate animals: D13-087-7). Sixteen baboons, 10 males and six females, ranging in age
141 from 6 to 16 years were tested between August 2011 and March 2012 (see Appendix Table
142 A1). All subjects lived in reproductive social groups comprising one adult male, two to five
143 adult females and their immature offspring (up to 2 years old). Groups had free access to 14

144 m² outdoor areas connected to 12 m² indoor areas. The enclosures were enriched by wooden
145 platforms and vertical structures of different heights, in both the outdoor and indoor areas. All
146 monkeys were fed four times a day with industrial monkey pellets, seed mixture, fresh
147 vegetables and fruits. Water was available ad libitum and subjects were never deprived of
148 food or water during testing. Subjects were tested in their outdoor area, and only females were
149 partly isolated from dominant individuals (which were kept inside) during testing. The
150 experimental procedure complied with the current French laws and the European directive
151 86/609/CEE. According to Article 3 (definitions) of the current European directive, this
152 experiment does not qualify as an experimental procedure and therefore does not require
153 institutional ethics approval.

154

155 <H2>*Apparatus*

156

157 Prior to each test session, we placed inside the cage a concrete block perpendicularly to the
158 mesh, at about 90 cm from the ground so that subjects could gesture at about the height of a
159 person. The mesh was equipped with a 10x60 cm opening through which the baboons could
160 freely pass their arms. During testing, a Plexiglas panel of 80x35 cm with two 10x15 cm holes
161 separated by 25 cm from centre to centre was fixed to the mesh over the opening (see
162 Supplementary Videos S1–S4). This panel was devised to facilitate subsequent recording of
163 baboons' gestures on video footage. Baboons were hence allowed to beg through the holes
164 towards an experimenter standing 1 m in front of the cage. Two video cameras were placed 2
165 m in front of the cage on both sides of the experimenter at an angle of 45° to the subject's
166 midline. All sessions were videotaped at a rate of 30 frames/s.

167

168 <H2>Test Procedure

169

170 All subjects were previously trained to beg through one of the holes of the Plexiglas panel to
171 request the food reward held in the experimenter's hand (see the Appendix for the full
172 procedure). Baboons were then tested for their requesting behaviour in four conditions. In the
173 control condition, the condition Out, the experimenter deposited a piece of banana (4 cm long
174 throughout the study) on the ground, 1 m in front of the cage, and left the test area (see
175 Supplementary Video S1). In the other three conditions, the test conditions, the experimenter
176 stood 1 m in front of the cage holding a piece of banana in one hand always in sight of the
177 subject: (1) Eyes open: the experimenter faced and looked at the subject (see Supplementary
178 Video S2); (2) Eyes closed: the experimenter faced the subject but kept her eyes closed (see
179 Supplementary Video S3); (3) Back turned: the experimenter was oriented away from the
180 subject but held the food behind her back (see Supplementary Video S4). Note that the
181 experimenter did not stare at the baboons in the Eyes open condition but rather looked
182 alternately to the eyes and the upper part of the nose so as to avoid possible fear reactions.
183 Each test session comprised four 30 s experimental trials alternated with eight motivation
184 trials in which the experimenter offered the subject the food as soon as it requested it. At the
185 end of each 30 s experimental trial, the experimenter gave the subject the piece of banana
186 regardless of its behaviour during the trial. Each baboon received four test sessions (one per
187 day), each experimental condition being presented once per session. The order of exposure to
188 the four conditions was counterbalanced between subjects and sessions; four distinct random
189 orders of conditions were presented to four groups of four subjects using a Latin square
190 procedure so as to control for possible habituation to the procedure (see full details in
191 Appendix Table A2).

192

193 <H2>*Data Scoring and Reliability*

194

195 Two different types of manual gestures were observed during the study and scored on the
196 videos for further analysis. Begging gestures were visual gestures consisting of extending one
197 or two arm(s) with fingers and hand(s) being in line with the arm(s) (Fig. 1). Attention-getting
198 gestures were auditory-based gestures consisting of banging the Plexiglas panel. Visual
199 orienting behaviour that took the form of gaze alternation bouts between the experimenter's
200 face and the food was also recorded. A first main observer coded all occurrences of begging
201 gestures and attention-getting behaviours at 30 frames/s using a VLC media player. A
202 begging gesture started when the wrist crossed the mesh and ended with the partial or
203 complete withdrawal of the arm. A new occurrence was scored whenever the subject brought
204 its arm back, with the elbow being inside the cage, and extended it again. A new occurrence
205 of attention-getting gesture was scored each time the subject banged the Plexiglas panel
206 producing distinct sounds. A second main observer coded all occurrences of visual orienting
207 behaviour frame by frame using Avidemux 2.5 (32-bit). Gaze alternation bouts were recorded
208 based on the conservative number of four consecutive looks alternating between the
209 experimenter's face and the piece of banana. For reliability purposes, 15% of the video
210 material was randomly assigned to two novel observers who were naïve to the experiment.
211 This resulted in a total of 40 experimental trials, each of 30 s, in 10 different test sessions.
212 One novel observer coded the begging and attention-getting gestures while the other coded
213 gaze alternation bouts. Reliability was assessed within pairs of main and novel observers and
214 was high for both gestures (Cohen's $k = 0.82$) and gaze alternation bouts (Cohen's $k = 0.76$).

215

216 <H2>*Statistical analysis*

217

218 We used an approach of multimodel inference to determine which cues to attention most
219 affected the responses of the subjects (Burnham & Anderson, 2004). We processed the
220 numbers of begging gestures, attention-getting gestures and gaze alternation bouts produced
221 by the 16 subjects over all test sessions across experimental conditions. Missing data occurred
222 for one subject (Tulie) in the last test session and were considered as such in the models. We
223 followed a three-step procedure: (1) we fitted several models varying the nature of cues to
224 attention as fixed effects (Table 1); (2) we selected the models that best fitted the observed
225 data; and (3) we performed tests of significance on the retained models.

226

227 <H3>*Model fitting*

228 As the frequency distribution of all dependent variables was not normal, we selected a
229 Poisson family with a log link function adapted to count data for fitting generalized linear
230 mixed models with ‘condition’ as fixed effect (i.e. Main Models). Pseudoreplication caused
231 by repeated observations of the same individual was taken into consideration by adding the
232 individual as a random effect. Second, we examined the possible variation of behavioural
233 responses over time (habituation) by fitting models with the interaction between ‘condition’
234 and ‘block’ of test sessions as fixed effects and ‘individual’ and ‘block’ as random effects (i.e.
235 Time Models). The first two test sessions were pooled as block 1 and the last two test sessions
236 as block 2. Third, we tested which postural cues to attention had the strongest effect on
237 dependent variables by performing nested models of the parameter ‘condition’ (i.e. Nested
238 Models). This procedure allowed us to weight the relative influence of the different cues to
239 attention (e.g. state of the eyes, body orientation) ‘nested’ in the parameter ‘condition’, and

240 advantageously replace traditional post hoc comparisons. To test whether the effect of the
241 state of the eyes could be stronger than the effect of head and body orientation, we pooled the
242 Eyes closed and Back turned conditions into condition Cannot see to compare with condition
243 Can see (i.e. Eyes open). To test whether the effect of head and body orientation could be
244 stronger than the effect of the state of the eyes, we pooled the Eyes open and Eyes closed
245 conditions into condition Front to compare with condition Back (i.e. Back turned).

246

247 <H3>Model selection

248 For each dependent variable we proceeded to select the best fitting models on the basis of the
249 lowest AICc (i.e. Akaike information criterion corrected, Table 1), which applies a second-
250 order correction adapted to small samples (Burnham & Anderson, 2004).

251

252 <H3>Test of significance

253 We used chi-square tests of the log-likelihood ratios to test whether the retained models fitted
254 the observed data significantly better than a hypothetical null model in which no fixed effect
255 had been implemented (Brown & Prescott, 2006). All tests were two tailed and were
256 performed with R 2.10.1 software (<http://cran.r-project.org>) with level of significance set at
257 0.050.

258

259

260 <H1>Results

261

262 <H2>Recognition of Recipient's Visual Attention

263

264 The baboons adjusted their begging behaviour to the visual attentional state of the
265 experimenter (Fig. 2). The experimental condition most affected the number of begging
266 gestures (Table 1, Main Model). Baboons gestured more when the experimenter had her eyes
267 open than in the other three conditions, Eyes closed (Wald test: $z = -2.28$, $P = 0.023$), Back
268 turned (Wald test: $z = -9.30$, $P < 0.001$) and Out (Wald test: $z = -11.64$, $P < 0.001$). Body
269 orientation by itself (Table 1, Front/Back Model) and the state of the experimenter's eyes
270 alone (Table 1, Can see/Cannot see Model) were not better predictors of subjects' responses
271 than experimental conditions mixing both cues (Table 1), suggesting that both played a role in
272 the understanding of attentional state by baboons. In a transfer test performed by novel
273 experimenters so as to exclude possible conditioned responses driven by the sight of the main
274 experimenter, baboons showed very similar responses (see the Appendix and Fig. A1).

275

276 The baboons displayed significantly more gaze alternation bouts (Table 1, Main
277 Model: Fig. 3) when the experimenter had her eyes open than when her eyes were closed
278 (Wald test: $z = -2.13$, $P = 0.033$) or when her back was turned (Wald test: $z = -6.41$, $P <$
279 0.001). Body orientation by itself (Table 1, Front/Back model) and the state of the
280 experimenter's eyes alone (Table 1, Can see/Cannot see model) were not better predictors of
281 subjects' responses than experimental conditions mixing both cues (Table 1) suggesting that
282 both played a role in the understanding of attentional state by baboons.

283

284 <H2>*Attraction of Recipient's Visual Attention*

285

286 Of the 16 subjects, 14 displayed attention-getting gestures, i.e. auditory-based gestures
287 consisting of banging the apparatus. Banging was more frequent when the experimenter was
288 present than when she was absent (Wald test: $z = -4.22$, $P < 0.001$), and when the
289 experimenter could not see the subject than when she could (Wald test: $z = 0.029$, $P = 0.029$),
290 during the first two test sessions only (Table 1, Can See/Cannot See Nested Model).
291 Restricting our analysis to these two sessions in which no habituation to the procedure was
292 likely to occur, we found that baboons performed more banging when the experimenter could
293 not see them than when she could (one-sample permutation test: $t = 2.09$, $P = 0.021$; Fig. 4).
294 Body orientation of the experimenter either alone (Table 1, Front/Back Model) or in
295 combination with the state of her eyes (Table 1, Main Model) were not better predictors of the
296 subjects' banging than being seen or not by the experimenter (Table 1).

297

298 <H2>*Adjustment of Gestures to Recipient's Visual Attention*

299

300 Considering the first two test sessions, we investigated whether subjects favoured visual
301 requests (food-begging gestures) over auditory-based gestures (banging) when the
302 experimenter could see them compared to when she could not. Gesture types produced by the
303 baboons were affected by the possibility of being seen by the experimenter (Fisher's exact
304 probability test: $P < 0.001$). Baboons made more visual requests when the experimenter could
305 see them than when she could not. Conversely, they banged more when the experimenter
306 could not see them than when she could (Fig. 5).

307

308 <H1>**Discussion**

309

310 Three novel findings resulted from this study. First, baboons tailored communicative signals
311 from different modalities as a function of a human's visual attention based on the state of the
312 eyes. Second, gestures were accompanied by gaze alternation between the human's face and
313 the food. Third, monkeys spontaneously elaborated attention-getting signals when there was a
314 communication breakdown. Until now, this latter ability was considered as a feature unique to
315 communication of humans and great apes. Collectively, these findings provide solid evidence
316 that baboons understand the state of the eyes in others' visual attention and use requesting
317 gestures intentionally.

318 The primate brain contains neurons that are selectively responsive to eye direction,
319 head orientation and body orientation, possibly as part of a hierarchical process for
320 determining the direction of another's attention (see Emery, 2000 for a review). In baboons,
321 the eye region is the primary focus of attention during processing of both humans' and
322 conspecifics' faces (Martin-Malivel, Mangini, Fagot, & Biederman, 2006) and is essential for
323 face recognition (Kyes & Candland, 1987). Monkeys also distinguish directed from averted
324 gazes from both a conspecific and a human (Keating & Keating, 1982) and they follow the
325 gaze direction of other individuals (Tomasello, Call, & Hare, 1998), sometimes relying on eye
326 gaze direction only (e.g. in rhesus macaques, *Macaca mulatta*: Lorincz, Baker, & Perrett,
327 2000; in baboons: Vick, Bovet, & Anderson, 2001). Furthermore, monkeys use humans' state
328 of the eyes as a cue to adjust behaviour in competitive situations (e.g. Flombaum & Santos,
329 2005; Vick & Anderson, 2003). It is therefore puzzling that sensitivity to others' state of the
330 eyes has hardly ever been evidenced in a communicative context, except in a few studies
331 (Hattori et al., 2010; Hostetter et al., 2007;). Here, we found that baboons performed virtually
332 no gestural behaviour when the human was absent, but produced most visual gestures when
333 the human was facing them with her eyes open. This suggests that their requesting behaviour

334 was not merely driven by the sight of the food. Instead, it appears to be genuine
335 communication motivated by the presence of the human partner. Moreover, while the
336 information provided by the head and body orientation may be sufficient for interpreting
337 direction of attention in quadrupedal species (Emery, 2000), this study shows that baboons
338 also use open eyes as a cue when it is available in a communicative context.

339 In one study very similar to ours, Kaminski et al. (2004) pointed out a hierarchical use
340 of cues to attention by chimpanzees. The apes responded primarily to body orientation and
341 secondarily to face orientation only when the experimenter's body was oriented towards
342 them. The present study did not allow us to distinguish between the possibly hierarchical
343 contribution of head and body cues. However, the baboons responded more with visual
344 signals to the Eyes closed than the Back turned conditions, and neither body orientation by
345 itself nor the state of the experimenter's eyes was a better predictor of the subjects' begging
346 for food than the Eyes open condition which mixed both cues. This suggests that not only the
347 state of the eyes but also body and head orientation were relevant cues to others' visual
348 attention for olive baboons. However, it remains possible that baboons respond to the state of
349 the eyes only when the human's body is oriented towards them.

350 If our findings seem contradictory to certain previous studies in which food was
351 deposited on a platform (e.g. Kaminski et al., 2004; Povinelli & Eddy, 1996), they do
352 corroborate the findings from other studies in which food was held in the experimenter's hand
353 (e.g. Hattori et al. 2010; Hostetter et al. 2007). This slight methodological difference may
354 therefore deserve further discussion. As previously stressed for great apes, body orientation,
355 but not face orientation, may convey information about the experimenter's physical ability to
356 give food rather than information about her ability to perceive a visual signal (Kaminski et al.,
357 2004; Tempelmann et al., 2011). We suggest that holding food in the hands may increase and
358 keep constant the disposition of the human to give food regardless of body orientation. Under

359 such circumstances, it is possible that subjects process more subtle cues to attention such as
360 the open versus closed state of the experimenter's eyes when begging for food. In a similar
361 experiment, capuchin monkeys, *Cebus apella*, successfully adjusted their requesting gestures
362 to the attentional state of a human holding food in one hand, but failed to adjust their
363 requesting gestures to the attentional state of a human when gestures had to be directed at
364 food deposited on a table (Hattori et al., 2010). While both gestures are communicative,
365 pointing towards food on a table appears to be a rather difficult task for monkeys (e.g. Hattori
366 et al., 2010). More research is hence needed to understand whether pointing towards an
367 external target and begging from an experimenter require differential cognitive means for
368 attracting the partner's attention.

369 Wild baboons have been reported to use visual orienting behaviour to attract a
370 partner's visual attention. For instance, they solicit help in conflicts by looking alternately to
371 an opponent and a solicited helper (Packer, 1977). Here, we report evidence of gaze
372 alternation supporting gestural communication that was tuned to the visual attention of the
373 recipient. Gaze alternation has long been considered as a cornerstone of the development of
374 intentional communication in human infants (Bates et al., 1975; Camaioni et al., 2004; Franco
375 & Butterworth, 1996). In line with a previous study (Meunier et al., 2012), our baboons
376 displayed visual orienting behaviour that was related not only to the locations of the social
377 partner and the object of interest, but also to the state of the eyes of the experimenter. This
378 suggests that baboons understand others' visual attention as a prerequisite for coordinating
379 their own attention with that of others towards an external target. This is reminiscent of
380 children developing joint visual attention (Butterworth, 2004).

381 However, the fact that the state of the eyes is not always used as a cue by nonhuman
382 primates to infer attention direction (e.g. Kaminski et al., 2004; Maille et al., 2012; Povinelli
383 & Eddy, 1996), or when it is used it does not necessarily supplant head and body cues (e.g.

384 this study), has led some to contrast simple learning of cues to attention with actual
385 understanding of visual attention (Gómez, 1998; Povinelli & Eddy, 1996). In this respect, it is
386 likely that, owing to explicit training, baboons discriminated cues to the Eyes open condition
387 as cues that increased the likelihood of getting the reward. However, neither visual orientating
388 nor attention-getting behaviour was explicitly trained in the present study, yet it was flexibly
389 adjusted to the visual attention of the experimenter. Baboons produced more visual gestures
390 and visual orienting behaviours, but fewer attention-getting gestures when the experimenter
391 could see them than when she could not. Whether baboons had implicitly learned these cues
392 to attention during training or through prior experience, which may result in implicit
393 knowledge of others' visual attention, is not possible to disentangle here. Whatever the
394 operating process, it most probably led to an increased understanding of the conditions under
395 which their communicative signals can be effective.

396 The use of acoustic communication (i.e. including vocalizations, nonvoiced sounds or
397 bimodal communication such as visual/auditory-based gestures) as a means of attracting the
398 attention of an otherwise inattentive partner has been reported in chimpanzees (Hopkins,
399 Taglialatela, & Leavens, 2007; Hostetter et al. 2007; Leavens et al. 2004), although not found
400 in all studies (Tempelmann et al., 2011; Theall & Povinelli, 1999). To our knowledge, our
401 results are the first report of monkeys producing gestures as a means of elaborating
402 communication that failed to elicit the desired outcome. We thus propose that baboons
403 possess flexible communicative means that they can use with the same intent, although the
404 present study did not systematically manipulate the expected outcome of the communicative
405 exchange (but see Leavens et al., 2005). In contrast to a previous study that found baboons
406 banged the cage as a result of frustration (Meunier et al., 2012), the behavioural pattern
407 observed here does not result from thwarted communicative bids only, as evidenced by
408 differential responses as a function of condition (owing to the fact that all experimental trials

409 lasted for only 30 s and were systematically rewarded). Baboons produced more auditory-
410 based gestures but fewer visual gestures when the experimenter could not see them,
411 suggesting they might have used auditory communication as a substitute for visual
412 communication to capture the attention of the experimenter.

413 This study brings critical insight to the interplay between intentional communication
414 and social understanding through the primate lineage. Human infants (Liszkowski, Albrecht,
415 Carpenter, & Tomasello, 2008) and chimpanzees (Hopkins et al., 2007; Hostetter et al., 2007;
416 Leavens et al., 2004) are known to use vocalizations as a means of recruiting their partner's
417 attention. Here, we emphasize that Old World monkeys are also capable of shifting to
418 acoustic communication when the recipient is not visually attending. In contrast to human
419 infants and chimpanzees, this acoustic communication is purely gestural, not vocal. This
420 finding questions the evolutionary emergence of vocal intentional communication in the
421 primate lineage. Intentional acoustic communication might have been 'scaffolded' onto the
422 special intent to attract others' attention (see Falk, 2004), initially through gestural
423 communication in Old World monkeys and progressively through both gestural and vocal
424 communication in great apes, before turning out predominantly vocal in early humans. Future
425 research may address this topical question of whether acoustic intentional communication
426 might have appeared in evolution concomitantly to the understanding of another's attention.

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428

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432 anonymous referees for their valuable comments on the manuscript.

433 **Supplementary Material**

434

435 Supplementary material is available, in the online version of this article, at doi

436

437 **References**

438

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580

581 **Appendix**

582 *Training of the subjects*

583 All subjects took part in training trials. The procedure comprised three steps in which the
584 experimenter stood in front of the cage of the focal subject holding a raisin in her open palm
585 in front of the subject, while progressively increasing the distance to the cage. In the first step,
586 the raisin was kept within the reach of the subject who extended one arm to grasp it in the
587 experimenter's hand. In the second step, the distance increased up to the limit of being out of
588 reach and the experimenter anticipated the attempt of the subject to reach the food in giving
589 the subject the raisin each time the subject initiated an arm extension out of the cage. In the
590 third step, the experimenter stood out of the subject's arm reach and went on giving the
591 subject the raisin immediately after each initiation of arm extension. For the arm extensions
592 being considered as begging gestures, we set postural criteria ensuring that manual actions
593 were no longer mechanically effective: (1) the subject had not to try to grasp the raisin by
594 rotating its shoulder so as to go further through the wire mesh; (2) the subject's fingers had to
595 be extended in line with the hand and the arm. Subjects had to reach the criterion of 80% of
596 valid gestures across three consecutive 10-trials sessions administered once a day.

597

598 *Replication with novel experimenters*

599 Two extra test sessions were performed with novel experimenters so as to exclude possible
600 conditioned responses driven by the sight of the main experimenter. Baboons were presented
601 once to a novel woman and once to a novel man in a 2 by 2 design relying on the
602 experimenter's novelty (main experimenter versus novel experimenters first) and
603 experimenter's sex (novel woman versus novel man first). Experimental procedure and data
604 analysis were similar to those for the main experiment.

605 Baboons showed similar behavioural trends when they were tested with novel
606 experimenters over two test sessions (see Appendix Fig. A1). They adjusted their begging
607 behaviour to the visual attentional state of the experimenter (Main Model: AIC = 156.4; chi-
608 square tests for the log-likelihood ratios: Main Model – Null Model: $P < 0.001$). Baboons
609 produced significantly more gestures in the Eyes open than in the Back turned (Wald test: $z =$
610 -4.20 , $P < 0.001$) and Out (Wald test: $z = -6.47$, $P < 0.001$) conditions, but not in the Eyes
611 closed condition (Wald test: $z = -1.14$, $P = 0.253$).

612 Body orientation by itself (Front/Back Model: AIC = 155.7) may consequently be a
613 better predictor of subjects' responses than experimental conditions mixing both cues,
614 although the two models did not differ significantly (chi-square tests for the log-likelihood
615 ratios: Main Model – Front/Back Model: $P = 0.251$). However, the state of the experimenter's
616 eyes was not an accurate predictor of the subjects' responses (Can see/Cannot see Model: AIC
617 = 164.5; chi-square tests for the log-likelihood ratios: Main Model – Can see/Cannot see
618 Model: $P < 0.010$).

619 These findings support the proposal that baboons' gestural communication is driven
620 not by the sight of the food reward alone nor by the sight of the main experimenter who could
621 have been associated with the delivery of the reward. We propose that baboons' begging
622 gestures should be interpreted as genuine communicative attempts motivated by the presence
623 of a partner whose cooperation is required to get the reward. Further testing is, however,
624 needed to find out whether baboons processed well-known and novel faces differently and
625 whether such differential treatment may explain why they did not rely on the state of the
626 novel experimenter's eyes to adjust their communicative behaviour in this experiment.

627

628 Table 1. Summary of the models fitted for each dependent variable

Model name	Fixed effect	Random effect	AICc	Δ AICc	Significance
Dependent variable: number of begging gestures					
Null Model	None	Individual	812.10	510.11	***
Main Model	Condition	Individual	301.99	0.00	/
Time Model	Block, condition, block:condition	Individual:block	308.70	6.71	NS
Front/back Nested Model	Condition	Individual	305.19	3.20	*
Can see/cannot see Nested Model	Condition	Individual	356.19	54.20	***
Dependent variable: number of gaze alternation bouts					
Null Model	None	Individual	281.70	45.21	***
Main Model	Condition	Individual	236.49	0.00	/

629	Time Model	Block, condition, block:condition	Individual:block	246.40	9.91	NS
630	Front/back Nested Model	Condition	Individual	239.09	2.60	*
631	Can see/cannot see Nested Model	Condition	Individual	258.19	21.70	***
632	Dependent variable: number of attention-getting gestures					
633						
634	Null Model	None	Individual:block	409.80	123.00	***
635	Main Model	Condition	Individual	297.89	11.09	***
636	Time Model	Block, condition, block:condition	Individual:block	290.20	3.40	NS
637	Front/back Nested Model	Condition, block, condition:block	Individual:block	289.40	2.60	***
638	Can see/cannot see Nested Model	Condition, block, condition:block	Individual:block	286.80	0.00	/

639 Interactions between two effects are represented by colons. Bold characters indicate the retained model for each dependent variable. AICc:
640 Akaike information criterion with second-order correction; $\Delta AICc$: difference between the AIC of model i and the AIC of the retained model.
641 Chi-square tests for the log-likelihood ratios: * $P < 0.05$, *** $P < 0.001$.

642 Table A1. Subjects who participated in the study

643

Name	Sex	Age	Rearing history	Place of birth
Anelka	Male	6	Mother reared	Captivity
Katy	Female	16	Mother reared	Captivity
Marius	Male	14	Mother reared	Captivity
Momo	Male	14	Mother reared	Captivity
Oscar	Male	13	Mother reared	Captivity
Perfide	Female	12	Mother reared	Captivity
Prise	Female	12	Mother reared	Captivity
Raimu	Male	11	Mother reared	Captivity
Rambo	Male	11	Nursery	Captivity
Rodolphe	Male	11	Mother reared	Captivity
Sabine	Female	10	Mother reared	Captivity
Sestarde	Female	10	Mother reared	Captivity
Toti	Male	9	Mother reared	Captivity
Tulie	Female	9	Mother reared	Captivity
Ubu	Male	8	Mother reared	Captivity
Uranus	Male	8	Mother reared	Captivity

644

645

646

647 Table A2. Orders of exposure to experimental conditions

648

Subjects' group	First session	Second session	Third session	Fourth session
Group 1	Random order 1	Random order 2	Random order 3	Random order 4
Group 2	Random order 2	Random order 3	Random order 4	Random order 1
Group 3	Random order 3	Random order 4	Random order 1	Random order 2
Group 4	Random order 4	Random order 1	Random order 2	Random order 3

649

650 Random order 1: Eyes Open, Out, Eyes Closed, Back Turned; random order 2: Eyes Closed,
651 Eyes Open, Out, Back Turned; random order 3: Eyes Closed, Out, Back Turned, Eyes Open;
652 random order 4: Back Turned, Eyes Closed, Eyes Open, Out.

653

654

655

656 Figure captions

657

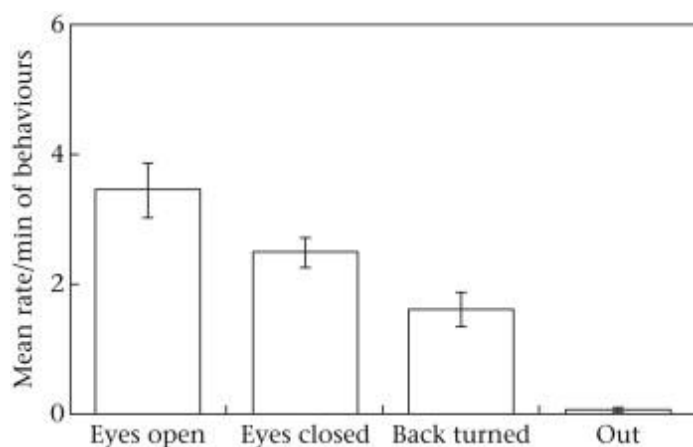
658 Figure 1. Begging gestures: (a) unimanual with the right hand and (b) bimanual.



659

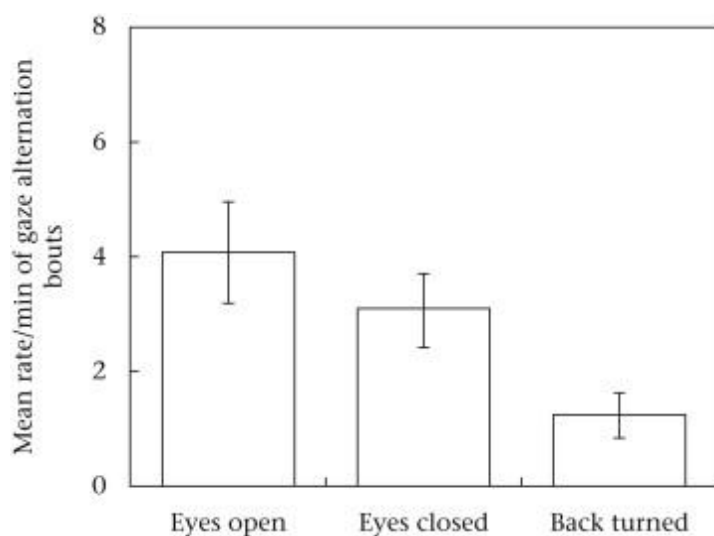
660

661 Figure 2. Mean rate/min \pm SEM of begging gestures for each experimental condition ($N = 16$
662 subjects).



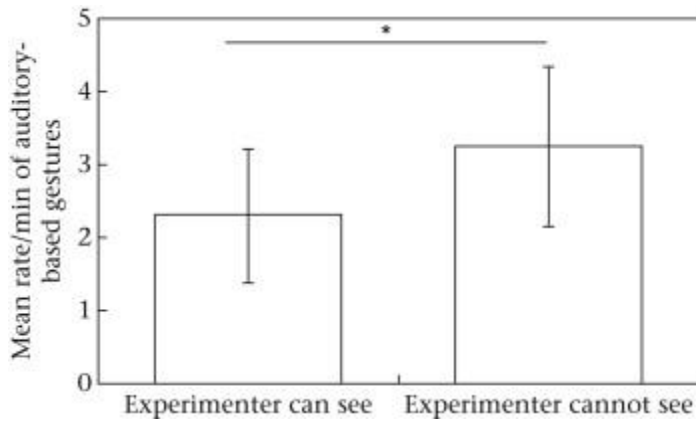
663

664 Figure 3. Mean rate/min \pm SEM of gaze alternation bouts for each experimental condition (N
665 = 16 subjects).



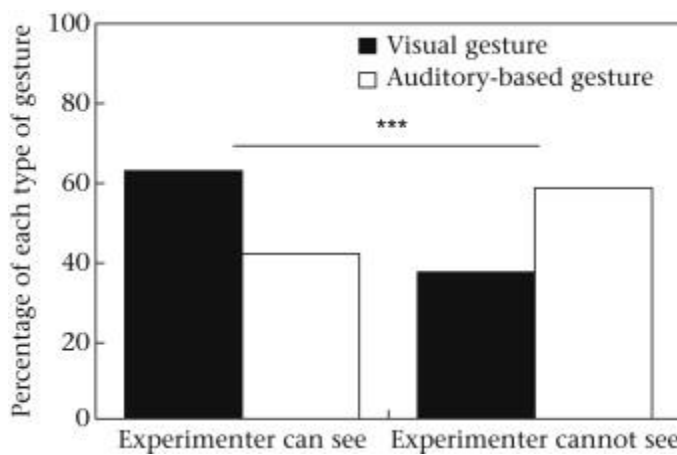
666

667 Figure 4. Mean rate/min \pm SEM of attention-getting gestures depending on experimenter's
668 visual attention during session block 1 ($N = 16$ subjects). One-sample permutation test: $*P <$
669 0.05.



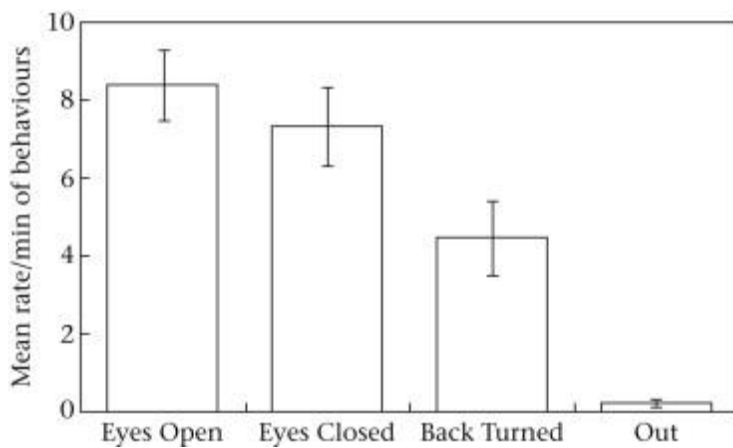
670

671 Figure 5. Percentages of visual and auditory-based gestures depending on experimenter's
 672 visual attention during session block 1 ($N = 16$ subjects). Fisher's exact probability test: $***P$
 673 < 0.001 .



674

675 Figure A1. Mean rate/min \pm SEM of begging gestures towards novel experimenters for each
 676 experimental condition ($N=15$ subjects).



677